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Two new hymenopteran fossils from the mid-Cretaceous of southern Africa (Hymenoptera: Jurapriidae, Evaniidae)

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ABSTRACT

The deposits at Orapa, Botswana, include several unique specimens of Hymenoptera that provide insights into relationships amongst various higher taxa, and insights into the probable characteristics of their ancestral forms. This paper describes two new monotypic genera and their type species. *Chalscelio orapa* Rasnitsyn & Brothers gen. et sp. n. shows characteristics of Chalcidoidea and Scelionidae, and may be a sister taxon to Chalcidoidea; it is provisionally placed in the family Jurapriidae. *Botsvania cretacea* Rasnitsyn & Brothers gen. et sp. n. shows a mixture of plesiomorphic and apomorphic characters when compared with other species of Evaniidae; its placement at or near the base of Evaniidae is highly probable, but greater certainty requires additional specimens.

KEY WORDS: Hymenoptera, Cretaceous, Gondwana, Botswana, new taxa, wasps.

INTRODUCTION

The lower Upper Cretaceous (Turonian) deposits at Orapa, Botswana, resulted from the kimberlitic eruption that formed a crater about 91 Mya, followed by accumulation of the fossiliferous sediments there (for details see Brothers & Rasnitsyn 2003, and references therein). The Orapa insect fossil assemblage is rich and diverse, currently being the most important source of information about the mid-Cretaceous insect world in the southern hemisphere (reviewed by Brothers & Rasnitsyn 2003). Unfortunately, our knowledge of the Orapa hymenopterans is as yet very poor, being limited, apart from the general review above, to the description of a vespid wasp (Brothers 1992) and some ants (Dlussky *et al.* 2004). The Orapa hymenopteran assemblage includes fossils of primary importance for understanding the higher-level evolution of the order. This paper is devoted to two fossils that provide information on the possible ancestries of the superfamily Chalcidoidea and the family Evaniidae (Evanioidea).

The fossils under study are currently housed in the Bernard Price Institute of Palaeontology (BP) at the University of the Witwatersrand, Johannesburg, South Africa.

TAXONOMY

Superfamily Serphitoidea Brues, 1937

Family Jurapriidae Rasnitsyn, 1983

Genus **Chalscelio** gen. n.

Figs 1, 2

Etymology: The genus name combines the names *Chalcis* and *Scelio*, alluding to the combination of characters both of Chalcidoidea and Scelionidae in the new genus; gender masculine.

Type species: *C. orapa* sp. n., by present designation.

Diagnosis: General appearance as in Scelionidae (Scelioninae), including female antenna clavate with 5 claval segments, geniculate and doubly angled (at apex of scape and before clava), and no anellus apparent; body elongate with long, fusiform, non-petiolate metasoma having 6 apparent segments and no sign of external ovipositor. Forewing venation generally typical of Scelionidae except for angular Cu, and combination of retained M (even if incomplete) and RS apparently lost beyond 2r–rs. Unlike Scelionidae and Platygastroidea in general, but highly reminiscent of Chalcidoidea, pronotum long medially but apparently shortened laterally and possibly not reaching tegula; forewing Cu distinctly angular at fork with M; number of antennal segments (13 evident, but 14 or even 15 possible because of imperfect preservation) low. (Position of antennal attachment (close to clypeus vs. far above it) unknown.)

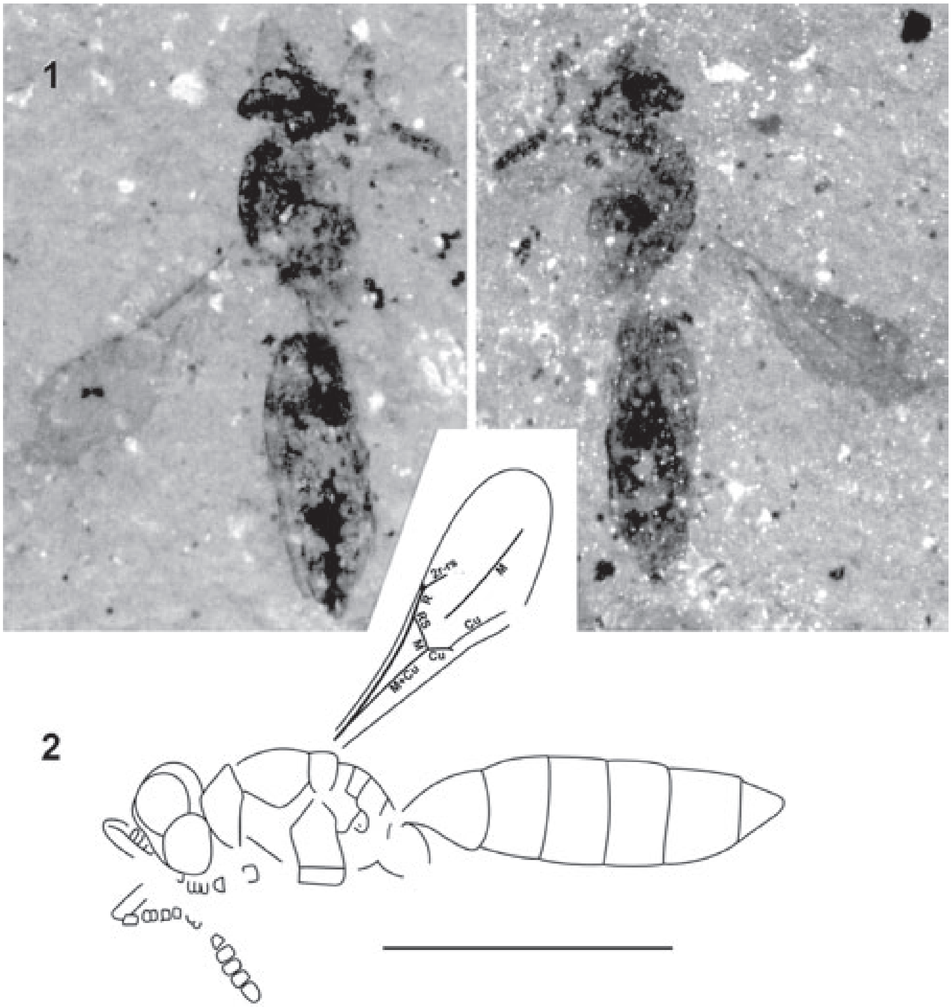
Species included: Type species only.

Phylogenetic position: As far as the characters available permit judgement, the fossil looks essentially like a scelionid, including the double-geniculate antenna, with only three but important anomalous characters, supposedly apomorphies of either Chalcidoidea or (Serphitoidea + Chalcidoidea) as interpreted by Rasnitsyn *et al.* (2004). One of these, putatively synapomorphic for (Serphitoidea + Chalcidoidea), is Cu distinctly bent posteriorly at its junction with M, a state never observed in Platygastroidea or Proctotrupoidea unless combined with cu–a displaced distal of the M+Cu junction (which is not the case here).

Another anomalous character is the medially long pronotum; this state is found in no Platygastroidea and is characteristic of Chalcidoidea. It was probably either independently gained, or independently inherited, by *Chalscelio* and Chalcidoidea directly from the predominantly Jurassic family Mesoserphidae (Rasnitsyn 1980, 1986).

The third character state, the pronotum short enough laterally not to reach the tegula, is tentatively inferred from extrapolation of the direction of the preserved forewing toward the mesosoma. The pronotum does not extend to the tegula in most Chalcidoidea because of the presence of an external prepectus between the two. If the pronotum truly does not reach the tegula in *Chalscelio*, this might imply a large, external prepectus, a feature only of Chalcidoidea. Otherwise, if it is the mesopleuron rather than a prepectus intervening between the pronotum and tegula, this might be a synapomorphy or, more likely, a homoplasy with *Microserphites* Kozlov & Rasnitsyn, 1979 (Serphitidae) and several fossil *Palaeomymar* Meunier, 1901 (Mymarommatidae) (cf. Kozlov & Rasnitsyn 1979, figs 7, 8, 10, 11).

As noted above, *Chalscelio* looks superficially like a female scelionid, notably in having a double-geniculate antenna with 5-segmented clava, apparently only six visible similar metasomal terga and a fusiform metasoma without evidence of an external ovipositor. Of these features, the antennal form is probably the strongest in possibly indicating a close relationship, the other features perhaps likely to be plesiomorphies. However, Rotoitidae, considered a basal lineage of Chalcidoidea, have a 6-segmented clava in the female (5-segmented in the male; other chalcidoids have a clava of three or fewer segments, rarely four; Gibson & Huber 2000), so the claval form in *Chalscelio* does not necessarily indicate a close relationship with Scelionidae. A complication is that Rotoitidae have a scelionid-like pronotum, short medially and reaching the tegula



Figs 1, 2. *Chalscelio orapa* Rasnitsyn & Brothers, gen. et sp. n.: (1) Holotype, BP/2/26990a and b/6, part and counterpart (slightly different scales); (2) Composite drawing; wing veins labelled conventionally. Scale bars = 1 mm.

laterally because the prepectus is linear and concealed under the hind margin of the pronotum, but it is uncertain whether that condition should be regarded as the groundplan for Chalcidoidea. Another complication is that Khutelchalcis Rasnitsyn, Basibuyuk & Quicke, 2004 from the lowermost Cretaceous of Mongolia, another possible basal chalcidoid (Rasnitsyn et al. 2004), shows a different combination of features characteristic of Scelionidae and Chalcidoidea: antenna lacking anelli but apparently with long multiporous plate sensilla and without scelionid-like bend; pronotum short medially and with prepectus not extending far dorsad, but with spiracle accommodated into posterodorsal excision of pronotum; venation essentially scelionid-like whilst metasoma chalcidoid-like (Fig. 3).

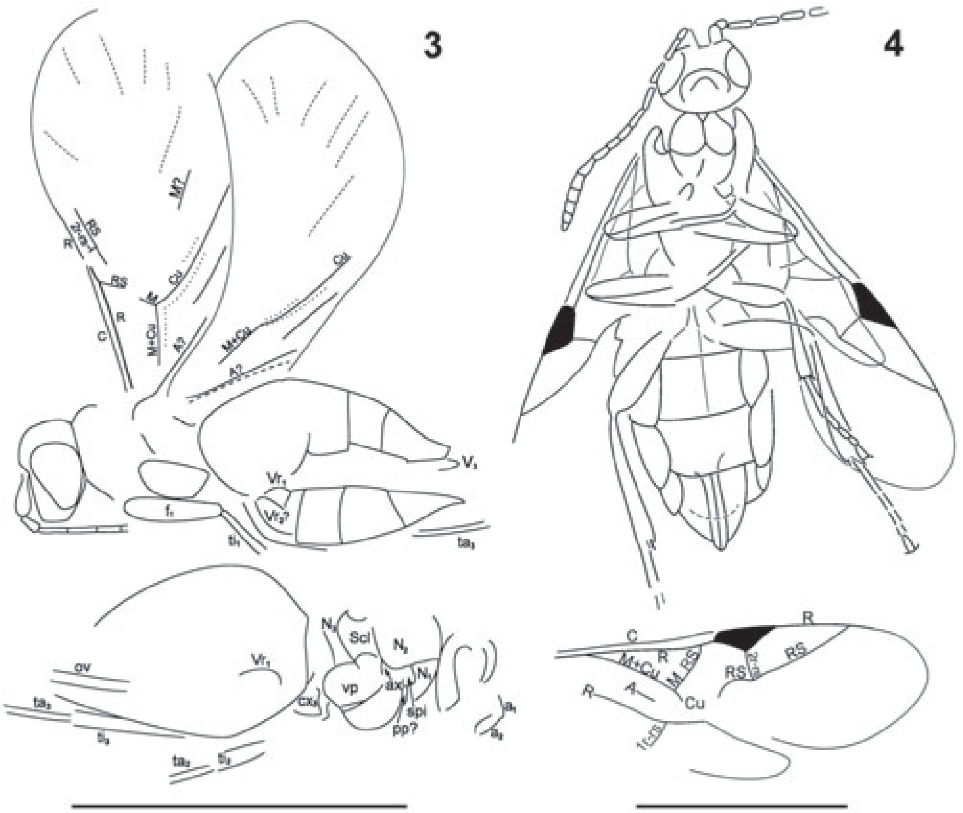
All the evidence taken together makes *Chalscelio* a possible sister group of Chalcidoidea. The basal position of *Chalscelio* with reference to Chalcidoidea is demonstrated by the plesiomorphic (not reduced ring- or tube-like) first metasomal segment, as well as by the wing venation retaining some plesiomorphic details (pterostigma, distal branch of Cu indicating a former connection with A). A sister-group rather than ancestral position is supported by a few venational autapomorphies in *Chalscelio*, such as the loss of RS connected with the 2r–rs crossvein, loss of the anal vein, and possibly loss of the costal vein enclosing the costal space (all of these being present in *Khutelchalcis*). All these autapomorphies are, however, of rather low phylogenetic importance, being common results of miniaturisation (reduction in body size). Numerous phylogenetically important characters (antennal sensilla, position of the mesothoracic spiracle with respect to the pronotum, external vs. internal ovipositor) are not determinable in *Chalscelio* because of the imperfect preservation of the unique fossil. Nevertheless, the available information leads to the conclusion that *Chalscelio* may be morphologically similar to the true chalcidoid ancestor. This characterises the fossil as a relict, because Chalcidoidea are now known from at least the earliest Cretaceous, that is they predate *Chalscelio* by some 40 to 50 million years.

Taxonomic position: This fossil is not a chalcidoid by any current definition, and yet it may be monophyletic with Chalcidoidea. However, to attribute *Chalscelio* formally to Chalcidoidea (naturally as a family of its own) would result in only a single character, the pronotum long medially and shortened laterally, as diagnostic of the resulting assemblage (except for Rotoitidae and Khutelchalcididae). This is impractical, particularly because knowledge of the fossil is incomplete. This is why, until more information is accumulated, we prefer to consider *Chalscelio* formally as a genus of questionable taxonomic position, tentatively grouped together with another such genus, *Jurapria* Rasnitsyn, 1983, for which the family name is already available (Rasnitsyn 1983; Rasnitsyn *et al.* 2004). *Jurapria* differs from *Chalscelio* in the antenna and general appearance, being less strikingly scelionid- or chalcidoid-like (Fig. 4), and in having the wing venation far more complete. Other important characters are hardly comparable because of the different preservation states of the two fossils: the pronotum form is unknown for *Jurapria*, while the position of the ovipositor, short and not tightly enclosed in *Jurapria*, is unknown for *Chalscelio*, although it may be similar or internal (but not long and exerted). The two genera are similar in two other important characters: both are synapomorphic with Serphitoidea + Chalcidoidea in having Cu arching or angular at the fork with M, and both are plesiomorphic with respect to them in having the first metasomal segment not modified into a tube or ring. This provides further justification for the present interpretation of their taxonomic position.

Chalscelio orapa sp. n.

Etymology: The species name, a noun in apposition, is the type locality.

Description: Body length 2.2 mm; forewing length as preserved (wing base perhaps incompletely visible) 1.2 mm. Ground colour moderately dark; head, flagellum, mesopleuron and metasoma darker. No surface sculpture evident. Head transverse, moderately wide (about as wide as mesosoma), with large, almost circular eyes occupying most of the sides. Temples narrow. Position of antennal sockets unknown. Antenna at



Figs 3, 4. (3) *Khutelchalcis gobiensis* Rasnitsyn, Basibuyuk & Quicke, holotype; drawing based on part (above) and counterpart (from Rasnitsyn *et al*. 2004); (4) *Jurapria sibirica* Rasnitsyn, holotype; drawing with fore- and hindwing below (modified after Rasnitsyn 1983). Abbreviations: a_1 – scape, a_2 – pedicel, ax – axilla, cx_3 – hind coxa, f_1 – fore femur, $ta_{2,3}$ –mid and hind tarsi, ti_{1-3} – fore, mid and hind tibiae, N_{1-3} – pro-, meso- and metanotum (the latter probably with metapostnotum delimited behind), ov – ovipositor, pp? – supposed prepectus, spi – spiracular excision of pronotum, Scl – mesoscutellum, vp – mesothoracic ventropleuron (ventral surface of mesothorax), Vr_1 – supposed upper margin of first valvifer, Vr_2 – second valvifer, V_3 – ovipositor sheath; wing veins labelled conventionally. In wing, dotted line – sharp concave furrow, dashed line – rounded convex fold. Scale bars = 1 mm.

least 13-segmented (number of flagellomeres not precisely known), twice bent (geniculate and bent basal to clava) and clavate. Scape several times longer than wide (full length unknown), wider than flagellum and narrower than clava. Pedicel about as wide as flagellar segments, about one and a half times as long as wide. No true anellar segments evident. Flagellar segments strongly transverse, at least 6 in number, of subequal length and width. Clava 5-segmented, with 1st segment subconical, only slightly wider than flagellar segments; subsequent segments of subequal width and length (except apical segment longer), subquadrangular, about 1.5 times as wide as long; apical segment narrowed toward rounded apex, 1.5 times as long as wide. Mesosoma ovate in dorsolateral view. Pronotum with apparently straight hind margin and weakly defined posterolateral angles. Mesonotum without distinct notauli (possibly because of insufficient preservation). Scutellum apparently wide and short. No distinct axilla evident.

Metanotum ribbon-like, not very short. Propodeum with two transverse lines, with lateral lines (probably incomplete below), and with ovate area surrounding spiracle. Forewing shorter than metasoma, narrow. Costal vein weak or lost. Pterostigma small, almost dot-like. Basal vein weakly oblique, separated from 2r–rs by slightly less than its length; 2r–rs oblique, slightly shorter than its distance from basal vein. No RS present (except for part in basal vein). Distal part of M long, not connected with basal vein. Cu bent posteriorly at fork with M, then bent anteriorly at rudiment of vein formerly closing cell. No trace of cu–a or 1A. Metasoma fusiform, with segment length ratios about 1:0.7:0.7:0.7:0.8:0.5. No external ovipositor evident. Relation between apical tergum and sternum (tightly closing metasomal apex at rest or not) unknown, but at least not wide apart apically.

Holotype: BP/2/26990a and b/6, female (based on form of antenna), almost complete but lacking legs (except for hind coxa) and hind wings. BOTSWANA: Orapa; Upper Cretaceous, Turonian.

Family Evaniidae Latreille, 1802
Genus **Botsvania** gen. n.

Figs 5, 6

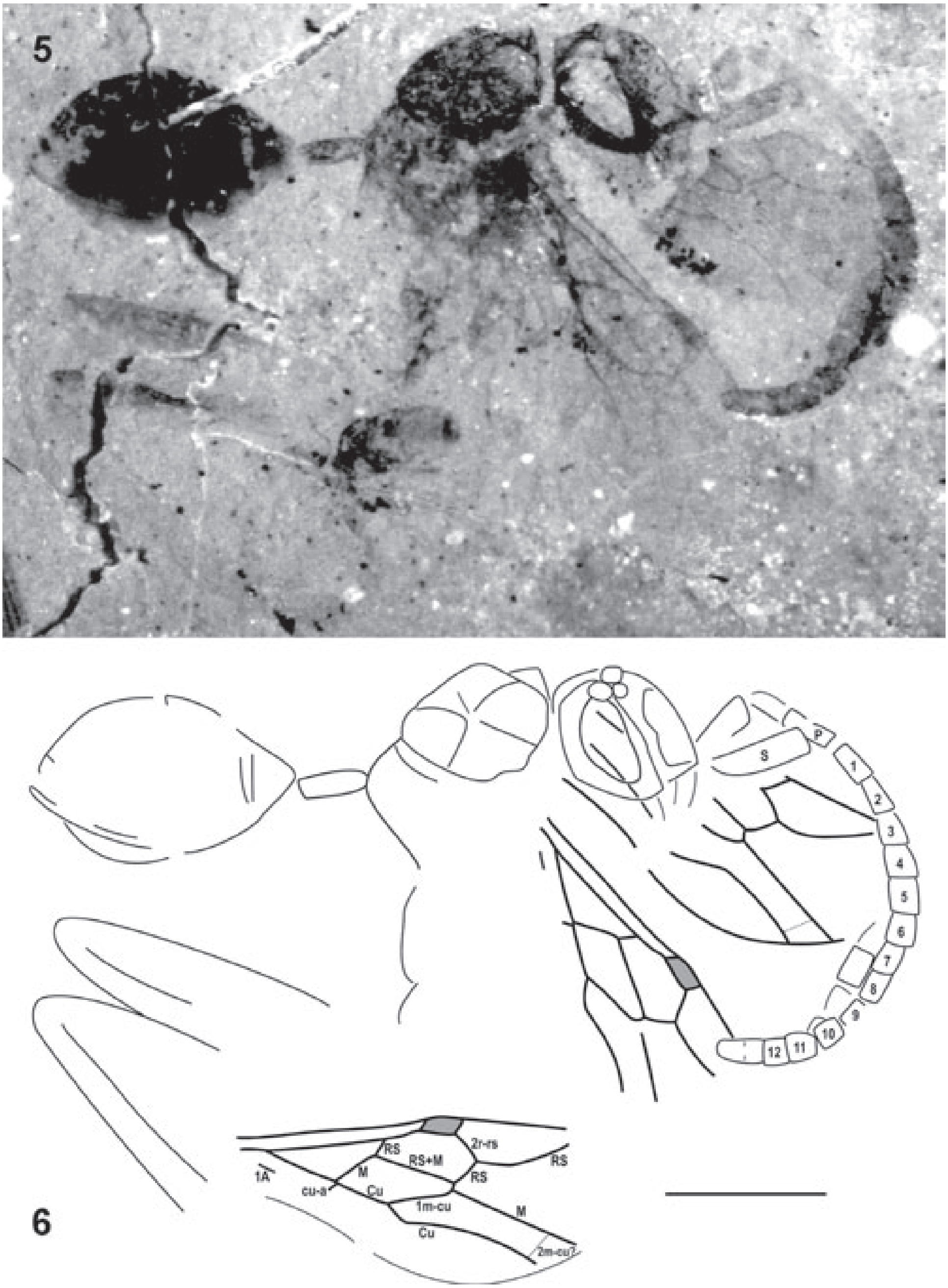
Etymology: The genus name is derived from Botswana and the genus *Evania*; gender feminine.

Type species: *B. cretacea* sp. n., by present designation.

Diagnosis: Antenna 15- or 16-segmented, attached near lower orbits. Mesothoracic prescutum and scutellum both triangular; lateral contour of propodeum smoothly rounded, with dorsal surface comparatively long (more than one third as long as posterior surface). Hind leg about as long as in some extant ensign wasps (hind femur as long as head and mesosoma combined). Vein RS+M originating much higher along basal vein than in most other Mesozoic evaniids. Petiolar (1st metasomal) segment subcylindrical, comparatively short and wide (length about 3 times width).

Species included: Type species only.

Taxonomic position: The position of the new genus within Evaniidae is supported by the high attachment of the metasoma on the propodeum (synapomorphy of Evanioidea) combined with the elbowed antenna (unique for Evaniidae in the superfamily), the close association of the head with the mesosoma, the absence of the medial mesoscutal line (present in Praeaulacidae), the position of RS+M well above the mid-height of the basal vein (not above mid-height in Gasteruptiidae s.l.), and the short subcylindrical petiole (conical if modified as a petiole in Gasteruptiidae s.l., long and subcylindrical in Andreneliidae). Within Evaniidae, the new genus combines some outstanding plesiomorphies (lower attachment of antenna, as in Evanioidea other than Evaniidae; triangular prescutum and scutellum, as in Praeaulacidae; and smoothly curved propodeum with comparatively long dorsal surface) with various apomorphies. The antenna with fewer than 25 segments (the number in *Mesevania* Basibuyuk & Rasnitsyn, 2000), the forewing crossveins 2–3r–m and 2m–cu lost as tubular veins, and the short ovipositor suggest monophyly with all evaniids other than *Mesevania*, while the 15- or 16-segmented antenna makes it possibly the sister group of all Evaniidae above *Mesevania* (fewer than 14 segments in all others; Basibuyuk *et al.* 2002, Deans *et al.* 2004). At the same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Figs 5, 6. *Botsvania cretacea* Rasnitsyn & Brothers, gen. et sp. n.: (5) Holotype, BP/2/26835/1; (6) Drawing, with composite forewing below. Antenna: S – scape, P – pedicel, 1–12 – flagellomeres; wing veins labelled conventionally. Scale bar = 1 mm.

time, the high position of RS+M suggests monophyly with higher Evaniidae, that is, with all Cainozoic genera plus the Late Cretaceous (Turonian) *Newjersevania* Basibuyuk, Quicke & Rasnitsyn, 2000. The remaining Cretaceous genera either have RS+M meeting the basal vein near its mid-height (*Mesevania*, *Lebanevania* Basibuyuk, Rasnitsyn, Fitton & Quicke, 2002, *Proparevania* Deans in Deans *et al.* 2004, and Grimaldivania Basibuyuk, Fitton, Rasnitsyn & Quicke, 2000b), or have their wing venation highly modified (the closely related *Cretevania* Rasnitsyn, 1975, *Procretevania* Zhang & Zhang, 2000, and *Eovernevania* Deans in Deans *et al.* 2004 have the basal vein displaced far basad, with the position of RS+M secondarily modified and variable). The comparatively long, narrow, subcylindrical petiole with no apparent borderline between tergum and sternum suggests monophyly with all Evaniidae except *Lebanevania* and *Grimaldivania*, in both of which it is short, stout and conical; the tergum and sternum are clearly delimited in *Lebanevania*. The general habitus with a short body and very long hind legs indicates a synapomorphy with the highest extant evaniids. Thus the phylogenetic indications are strikingly contradictory and might only be balanced by a cladistic analysis. However, the number of characters available is evidently too low to expect any meaningful results from a rigorous cladistic procedure (cf. the results obtained for the better-preserved amber fossils of *Lebanevania* and *Mesevania*; Basibuyuk *et al.* 2002, figs 9–14). Thus we can only conclude that the new genus has an undefined position among the lower (Cretaceous) Evaniidae.

Remarks: *Botsvania* is about coeval with *Grimaldivania* and *Newjersevania* from the Turonian of New Jersey in eastern North America. Those genera are represented by three species, and nothing similar to *Botsvania* has been found there. Similarly, seven other specimens of Evanioidea have been found at Orapa (Brothers & Rasnitsyn 2003), and not one of them is similar to *Grimaldivania* or *Newjersevania*. Also, nothing closely related has been found in numerous Late Cretaceous hymenopteran assemblages of Siberia; Evaniidae are represented there by *Cretevania* (Rasnitsyn, 1980). The older (Hauterivian through Albian) Evaniidae from the Lebanese and Burmese ambers are either unlike or (*Protoparevania*) only superficially similar to *Botsvania* (Basibuyuk *et al.* 2000*a*, 2002; Deans *et al.* 2004). The difference in mean size between impression fossils (from Orapa) and amber inclusions (from New Jersey and many Siberian localities) that often hinder comparison of respective fossil assemblages (Rasnitsyn, 1980), is of less importance in this particular case, because *Newjersevania casei* Basibuyuk, Quicke & Rasnitsyn, 2000 is even larger than *B. cretacea*, and small fossils less than 2 mm long are not uncommon in the Orapa assemblage. This makes it possible to conclude that the Late Cretaceous fauna of Evaniidae was diverse and zoogeographically specific, although not very rich at each particular place.

Botsvania cretacea sp. n.

Etymology: The species name, an adjective, refers to the Cretaceous period.

Description: Length of body 4.2 mm, antenna 3.4 mm, mesosoma 1.3 mm, forewing about 2 mm, hind femur about 2.0–2.2 mm, petiole 0.5 mm, rest of metasoma 1.7 mm. Ocular apodemes, mesonotum and metasoma beyond petiole dark; flagellum beyond 1st segment, head, much of remaining mesosoma, petiole, hind coxa and hind femur, dorsally, somewhat darkened; otherwise pale. No surface sculpture evident. Head with eyes large and elongate, occupying most of sides, with almost straight inner and convex outer orbits; ocelli large (indicating crepuscular to nocturnal activity). Mouthparts scarcely distinguishable. Antenna as long as meso- and metasoma combined, with scape almost 0.7 times as long as head capsule, about 3.5 times as long as wide, parallel-sided except narrowed basally over 0.3 of ventral contour. Pedicel narrower than scape, subcylindrical, about 1.5 times as long as wide. Flagellum 13- or 14- segmented (subdivision of apical segment not distinct), widest at and beyond middle, with segments gradually shortening toward apex, with 1st flagellomere twice as long as wide and 12th slightly transverse; apparently apical segment again twice as long as wide (if really double, true subapical segment distinctly transverse and true apical segment slightly longer than wide, narrowed toward rounded apex). Pronotum only partially preserved, apparently with straight anterior and deeply emarginate posterior margins, very short medially. Mesonotum almost symmetrical with respect to transscutal suture, with scutum between notauli and scutellum mirroring each other. Metanotum short, ribbon-like. Propodeum with declivity almost straight, about 2.5 times as long as horizontal surface (disc); junction of disc and declivity rounded. Hind coxa in-completely preserved, apparently elongate, not much shorter than height of pro-podeum. Hind femur and tibia long and narrow, femur about as long as metasoma, tibia apparently lacking irregular apical thickening (as described for *Mesevania*). No other leg parts preserved. Pterostigma fairly small, almost parallel-sided, with short oblique apex, 2r–rs originating near pterostigmal apex. Basal vein separated from pterostigma by about pterostigmal length, with RS forming less than its upper one-third. RS+M parallel to Cu (not to 2r–rs, as in many advanced Evaniidae); 2r–rs longer than abscissa of RS between it and RS+M (unlike in most Mesozoic Evaniidae except *Mesevania*). No rs–m crossveins present as tubular or nebulous veins. M meeting 1m–cu shortly after leaving RS+M (unlike in *Mesevania, Lebanevania*, and *Grimaldivania*); 1m–cu oblique, 2m–cu possibly present as weak nebulous vein placed near apical wing margin. Cu characteristically bent shortly beyond 1m–cu, but with no sign of connection to 1A there. Crossvein cu–a preserved as short stub just distal to M+Cu fork. Short section of 1A seen near wing base only. No hind wing apparent. Petiole with no apparent boundary between tergal and sternal parts, subcylindrical except narrowed basally over anterior quarter, 3 times as long as wide, as long as scutum. Rest of metasoma broadly fusiform, unknown if compressed, with basal segment almost triangular in lateral view, otherwise segmentation not evident. Ovipositor as preserved not extending beyond metasomal apex, slightly bent upward.

Holotype: BP/2/26835/1, female, almost complete fossil but lacking lower mesosoma, fore and mid legs and hind wings. BOTSWANA: Orapa; Upper Cretaceous, Turonian.

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